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Phytoplankton rate processes in coastal waters of the northern Gulf of Mexico and relationships to environmental conditions

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Abstract

Research describing phytoplankton rate processes and their relationship to environmental conditions is summarized. Relationships between P-I parameters and environmental variables in the region of study were significant in some cases, but variation between cruises made it difficult to generalize. Variability in ecological variables such as growth rate and cell size appeared to contribute to variations in pigment-specific photosynthesis-irradiance parameters. Our findings did support the view that a limited set of observations may be adequate to characterize P-I parameter distributions in a given region within a restricted period of time. Available data on photosynthetic parameters, in conjunction with irradiance and biomass (chlorophyll), provided input for a model to estimate areal distributions of primary production in relation to characteristics of the Mississippi River outflow plume and adjacent waters. Areal distributions of daily water column-integrated primary production ($\text{mg C m}^{-2} \text{d}^{-1}$), estimated using the P-I model, were spatially and temporally variable. Variability in magnitude, timing and circulation pattern of river discharge influenced the observed distributions of primary production. Productivity maxima occurred at intermediate salinities, presumably a consequence of increased light availability and decreased mixing/dilution rates. Highest productivities were observed during periods of warming and stratification in spring and late summer. Low productivities were attributed to low temperatures and relatively high rates of mixing in March 1991 and to reduced supply of river-borne nutrients in September 1991. An ocean color model to estimate primary production was evaluated. The model used an approach outlined in Morel and Berthon (1989), but with site-specific empirical relationships to estimate the integrated pigment in the water column from satellite detectable chlorophyll (C_{sat}) and site-specific trophic categories (oligotrophic to eutrophic) based on pigment concentration in the water column. Observed primary production versus production estimated by the satellite algorithm compared well. Sinking rates of particulate organic carbon (POC) from the photic zone showed no significant relationship to integrated primary production, but was strongly correlated with suspended particulate matter concentration. In addition, the ratio of primary production to POC export from the photic zone was highly variable. This was attributed, in part, to variations in phytoplankton species composition and grazing activities of microzooplankton and mesozooplankton. Taxon-specific growth and sedimentation rates of dominant phytoplankton provided evidence that in the northern Gulf of Mexico, phytoplankton rate processes proceeded very rapidly with growth rates primarily controlled by the supply of nutrients via the Mississippi River and the fate controlled primarily by size and density (silicification). Incorporation of ^{14}C into protein as well as analyses of chemical composition supported the idea that phytoplankton in the plume and shelf were growing at high relative growth rates and were adapted to low light levels.

Introduction

Primary production on the Louisiana continental shelf has been shown to be enhanced by nutrient-rich outflow from the Mississippi-Atchafalaya river system (Riley, 1939; Thomas and Simmons, 1960; Lohrenz et al., 1990). Nitrate concentrations in the lower Mississippi River have doubled since 1950 (Turner et al., 1987; Turner and Rabalais, 1991) leading to concerns that increases in primary production of fixed carbon coupled to increased nutrient loading (cf. Nixon et al., 1984) could result in significant perturbation of the northern Gulf of Mexico coastal ecosystem.

Possible consequences of this nutrient enhanced production include increased sedimentation of organic matter (e.g. Hargrave, 1973, 1975; Smetacek, 1984) resulting in greater likelihood for development of hypoxic conditions in benthic environments (Rabalais et al., 1992; Justic et al., 1993) and associated reduction in living resource yields. The impact of increased nutrient loading on carbon burial and shelf/sea transport could also have implications for studies of the global carbon cycle (e.g., Walsh et al., 1981, 1989).

Prediction of the coupling between nutrient loading, primary production, and export of organic matter from the photic zone requires quantification of these processes and the environmental and ecological factors which regulate them. Large environmental gradients characteristic of river-impacted coastal waters lead to significant variation in phytoplankton community production, growth and the vertical flux of particulate organic matter. Taxon-specific variations in phytoplankton production, growth and sinking may affect the quantity and quality of organic material reaching the sediments.

In 1990, the National Oceanic and Atmospheric Administration Coastal Ocean Program initiated the Nutrient Enhanced Coastal Ocean Productivity Program (NECOP) with a goal of understanding mechanisms of coupling between nutrient loading, magnitude and distribution of primary production, and formation of hypoxic bottom waters on the Louisiana shelf. Here we present a summary of our work investigating phytoplankton rate processes and their relation to environmental conditions.

Spatial and temporal variations of photosynthetic parameters in relation to environmental conditions in northern gulf of mexico coastal waters

The variable nature of primary production in this region has complicated efforts to discern temporal and spatial patterns of regional productivity and their relation to possible controlling factors. Improved temporal and spatial resolution of primary production distributions has been achieved by using photosynthesis-irradiance models (e.g., Fee, 1973a,b; Harrison et al., 1985). Such approaches require knowledge of the relationship of rates of pigment-specific photosynthesis to light, *i.e.*, the photosynthesis-irradiance curve (e.g., Jassby and Platt, 1976; Platt et al., 1980). Estimates of primary production can then be made from information about biomass and irradiance distributions, thereby allowing for more detailed sampling.

Environmental variability can act at the level of physiology within phytoplankton species as well as through effects on species composition to cause variations in photosynthesis-irradiance relationships. Such variation contributes to uncertainty in estimates of primary production derived using photosynthesis-irradiance models. Previous studies have demonstrated that photosynthetic parameters may vary over a wide range of temporal and spatial scales, with temperature and light being the most commonly observed environmental covariates (Platt and Jassby, 1976; Harrison and Platt, 1980; Malone and Neale, 1981; Falkowski, 1981; Cote and Platt, 1983). Diel periodicity (MacCaull and Platt, 1977; Harding et al., 1981, 1982) and species composition and cell size (Malone and Neale, 1981; Gallegos, 1992) have also been implicated as factors contributing to variability.

While variation in photosynthetic parameters in other coastal ecosystems has been examined, little is known about their spatial and temporal variation in the northern Gulf of Mexico. Such data can be used in the generation of modeled distributions of primary production over seasonal temporal scales and regional spatial scales (Lohrenz et al., 1992 and in prep.) and may facilitate understanding mechanisms of control at the ecosystem level. In addition, information about the distributions of photosynthesis-irradiance relationships may be incorporated into larger scale predictive models of primary production (e.g., Platt and Sathyendranath, 1988).

On a series of 8 cruises conducted in the northern Gulf of Mexico, efforts were made to characterize temporal and spatial variability in parameters of the photosynthesis-irradiance saturation curve (P_{\max}^B , α^B , I_k) and to relate the observed variations to environmental conditions (Lohrenz et al., in review). Experiments to examine the importance of diel variation in upper mixed layer populations were conducted in July-August 1990 and March 1991. During July-August 1990, P_{\max}^B and I_k showed significant increases and α^B decreased during the photoperiod in both river plume and shelf/slope populations. During March 1991, no consistent covariance of P-I parameters with local time was found, although highest values of α^B in the river plume were observed in early morning. Seasonal variation in P_{\max}^B and α^B (Table 1) were correlated with temperature (Fig. 1). Spatial variations of photosynthetic parameters in the upper mixed layer ranged 2-3 fold within any given cruise. For example, during the July-August 1990 cruise, values of P_{\max}^B and carbon-specific growth rates were higher in the river plume than in shelf waters (Fig. 2). In an effort to identify environmental regulatory factors, variations of photosynthetic parameters in the upper mixed layer were related to principal components derived from environmental variables including temperature, salinity, nutrients, mixed layer depth, attenuation coefficient and daily photosynthetically available radiation (PAR). Greater than 70% of the variation in the environmental variables could be accounted for by two principal components; the majority of this variation was associated with the first principal component, which was generally strongly correlated with salinity, nutrients, mixed layer depth, and attenuation coefficient. Correlations of P_{\max}^B , α^B , and I_k with the first principal component were found to be significant in some cases, an indication that spatial variability in P-I parameters was related to river outflow. Variation of P-I parameters in relation to depth and PAR were evaluated by regressions with principal components derived from depth, temperature and mean daily PAR. For most cruises, P_{\max}^B and I_k were negatively correlated with the first principal component, which was strongly positively correlated with depth and negatively correlated with daily PAR. This was consistent with a decrease in P_{\max}^B and I_k with depth that could be related to decreasing daily PAR. Positive correlations of α^B with the first principal component on two cruises, March 1991 and April 1992, indicated an increasing trend with depth. In conclusion, relationships between P-I parameters and environmental variables in the region of study were significant in some cases, but variation between cruises made it difficult to generalize. We attributed this variation to the physically dynamic characteristics of the region and the possible effects of variables that were not included in the analysis such as species composition. Our findings do support the view that a limited set of observations may be adequate to characterize P-I parameter distributions in a given region within a restricted period of time.

Seasonal variability in coupling between primary production and outflow of the Mississippi River on the Louisiana continental shelf

Information about the spatial and temporal distributions of primary production in the Mississippi River plume and adjacent waters is required for an understanding of the extent to which distributions of productivity are coupled to nutrient inputs from the river and the importance of control by other factors. Previous investigators have suggested that seasonal variations in the extent of the river-influenced region were likely to be substantial (e.g., Sklar and Turner, 1981). However, isolating seasonal patterns from time-series assessments of primary production of limited spatial extent are complicated by the dynamic and spatially heterogeneous nature of primary production in this region (Thomas and Simmons, 1960; Lohrenz et al., 1990), a consequence of the strong and variable gradients in physical and chemical properties.

Available data on photosynthetic parameters (Lohrenz et al., in review), in conjunction with irradiance and biomass (chlorophyll), provided input for a model to estimate areal distributions of primary production in relation to characteristics of the Mississippi River outflow plume and adjacent waters. Areal distributions of daily water column-integrated primary production, estimated using the P-I model, were spatially and temporally variable and exhibited varying degrees of coupling to riverine inputs (Fig. 3). Highest productivity was observed in July-August 1990 (Fig. 3a) and regions of elevated primary production were highest at intermediate salinities (Fig. 4a).

Productivity was uniformly low in March 1991 with the exception of one area to the west of the low salinity outflow water (Fig. 3b). Productivity was also low during September 1991, with the exception of a limited region of enhanced productivity in the vicinity of the restricted plume (Fig. 3c) corresponding to intermediate salinities (Fig. 4c). Finally, in April-May 1992 productivity was again higher (Fig. 3d) in the region of intermediate salinities (Fig. 4d).

Variability in magnitude, timing and circulation pattern of river discharge influenced the observed distributions of primary production. The pattern of high productivity at intermediate salinities (Fig. 4) has been observed previously in the Mississippi River outflow region (Lohrenz et al., 1990) and other coastal ecosystems, and presumably reflects increased light availability and decreased mixing/dilution rates. Highest productivities were observed during periods of warming and stratification in spring and late summer. Low productivities were attributed to low temperatures and relatively high rates of mixing in March 1991 and to reduced supply of river-borne nutrients in September 1991.

Primary production in the Gulf of Mexico coastal waters based on a remote sensing algorithm

Attempts to derive ocean-color based estimates of pigment and primary production in coastal waters have been complicated by the contributions of signals from non-pigment materials to the water leaving radiance. An ocean color model to estimate primary production was evaluated for coastal waters of the northern Gulf of Mexico (Prasad et al., in press). The model utilizes C_{sat} (mg m^{-3}) (a variable that accounts for the pigment sensed by the satellite sensor), photosynthetically available radiation (PAR, $\text{J m}^{-2} \text{d}^{-1}$) and a parameter, ψ^* (g Chl^{-1}), the water column chlorophyll specific cross-section for photosynthesis. C_{sat} and PAR were treated as variables while ψ^* was a site-specific parameter in the model. The model uses the approach outlined in Morel and Berthon (1989), but with site-specific statistical relationships to estimate the integrated pigment in the water column from C_{sat} and site-specific trophic categories (oligotrophic to eutrophic) based on pigment concentration in the water column. Observed production versus estimated production ($\text{mg C m}^{-2} \text{d}^{-1}$) for the pooled data compared very well (Fig. 5). ψ^* varied between 0.054 to 0.063 $\text{m}^2 (\text{g Chl})^{-1}$, a range comparable to that observed in other regions.

The relationship between primary production and the vertical export of particulate organic matter in a river impacted coastal ecosystem

One of the objectives of our study was to examine temporal variability in primary production relative to variations in rates of sinking of particulate organic matter from the euphotic zone in two regions: the Mississippi River plume and the inner Gulf of Mexico shelf (Redalje et al., in review). Observations during four research cruises, July/August 1990, March 1991, September 1991 and May 1992, revealed that photic zone integrated primary production varied significantly in both the river plume and shelf study regions, with greatest variability observed in the river plume region (Table 2). In the river plume and the adjacent shelf, highest production occurred during July/August 1990 ($8.17 \text{ gCm}^{-2}\text{d}^{-1}$ for the plume and $1.89\text{--}3.02 \text{ gCm}^{-2}\text{d}^{-1}$ for the shelf) and the lowest during March 1991 ($0.40\text{--}0.69 \text{ gCm}^{-2} \text{d}^{-1}$ for the plume and $0.12\text{--}0.45 \text{ gCm}^{-2}\text{d}^{-1}$ for the shelf). The vertical export of POC from the euphotic zone, determined with free-floating MULTITRAP sediment trap systems, also varied temporally in both study regions (Table 3), with highest values occurring in May 1992 ($1.80 \pm 0.04 \text{ gCm}^{-2}\text{d}^{-1}$ for the plume and $0.40 \pm 0.02 \text{ gCm}^{-2}\text{d}^{-1}$ for the shelf) and lowest values occurring during July/August 1990 ($0.29 \pm 0.02 \text{ gCm}^{-2}\text{d}^{-1}$ for the plume and $0.18 \pm 0.01 \text{ gCm}^{-2}\text{d}^{-1}$ for the shelf). Vertical export of POC showed no significant relationship to integrated primary production, but was strongly correlated with suspended particulate matter concentration (Table 5). In addition, the ratio of primary production to POC export from the photic zone was highly variable. This was attributed, in part, to variations in phytoplankton species composition and grazing activities of microzooplankton and mesozooplankton.

Taxon-specific growth and loss rates for dominant phytoplankton populations from the northern Gulf of Mexico

Taxon-specific growth and sedimentation rates of dominant phytoplankton were measured during two cruises (summer 1990 and spring 1991) in the northern Gulf of Mexico as part of NOAA's NECOP program (Fahnenstiel et al., 1992, and in review). Microzooplankton grazing rates were measured during the summer cruise. During each of the cruises, a series of stations from the Mississippi River mouth to the hypoxia region (located ca. 50-100 km west) were sampled to examine variability of growth and loss processes along a strong environmental gradient. Significant taxa- and group specific differences were noted for both growth and loss rates. Growth rates ranged from <0.1 - 3.0 d^{-1} with highest rates in the plume region during the summer cruise where surface rates were close to or exceeded previous μ_{max} values for several taxa. For all taxa, growth rates were lower in the hypoxia region than in the plume region and soluble nitrogen concentrations explained over 50% of the variability in growth rates. Diatom growth rates were similar to non-diatoms in the plume region but were significantly lower in the hypoxia region suggesting that silica limitation may exist in this region. The fate of phytoplankton appeared to be controlled by size and the degree of silicification. Significant microzooplankton grazing loss rates were noted only for small taxa ($<20\text{ }\mu\text{m}$). For microflagellates, microzooplankton grazing rates averaged 82% (range 42-214%) of the growth rate and sedimentation rates were always $<1\%$ of the growth rate. Sedimentation was an important loss for several diatoms with significant taxon-specific and seasonal differences noted. Large colonial diatoms, such as *Skeletonema costatum* and *Thalassiosira rotula* exhibited the highest sedimentation rates in the plume region during the spring cruise (0.2 - 1.0 d^{-1}) whereas the lowest rates ($<0.01\text{ d}^{-1}$) were noted for *Rhizosolenia fragilissima* and *Ceratulina pelagica* in the hypoxia region during the summer cruise. Our results suggest that in the northern Gulf of Mexico, phytoplankton rate processes proceed very rapidly with growth rates primarily controlled by the supply of nutrients via the Mississippi River and the fate controlled primarily by size and density (silicification).

The effects of environmental factors on phytoplankton physiological state and chemical composition

In addition to their impact on photosynthesis-irradiance parameters and the relationship between primary production and the vertical export of POM, changing environmental conditions can lead to variability in the chemical and biochemical composition of the phytoplankton present in the river plume and shelf regions. Seasonal variability in river discharge, and thus input of nutrients to the plume and shelf regions led to changes in the patterns of incorporation of ^{14}C into the major endproducts of photosynthesis - proteins, lipids, small molecular weight intermediates, and polysaccharides (Arwood, 1992). Predominate environmental conditions in the river plume (e.g., either nutrient-sufficient or phosphate-limited growth and low light adaptation) permitted phytoplankton populations to grow at or near their maximum growth rates, as indicated by high relative incorporation of ^{14}C into protein (DiTullio and Laws, 1983; 1986; Arwood, 1992). As the nutrient fields become depleted with distance from the plume, phytoplankton respond by increasing the incorporation of ^{14}C into lipids and small molecular weight intermediate compounds. However, even under relatively nutrient-depleted conditions, phytoplankton maintained the capacity to utilize the available nitrogen and synthesize protein.

Our results support the view that phytoplankton in the river plume and adjacent shelf waters appear to be limited by the availability of PO_4 which is in agreement with the suggestions of Ammerman (1992) and Smith and Hitchcock (1994). Samples obtained from the river plume and adjacent shelf waters were given various nutrient enrichment treatments (including the addition of PO_4 , NO_3 , SiO_3 , trace metals and vitamins in various combinations which included or excluded each of the components in standard f/2 medium concentrations; Chen, 1994). The phytoplankton responded with an increase in *in vivo* fluorescence when PO_4 had been added. The *in vivo* fluorescence response of treatments without added PO_4 were not different from that of the control treatments (e.g. no nutrient additions).

Chemical composition has frequently been used as an indicator of the physiological state of marine phytoplankton. Ratios of composition, such as C/chl *a* and C/N also provide useful information on environmental impacts on phytoplankton physiology. We investigated the responses of C/chl *a* and C/N for cultures of *Skeletonema costatum* and *Chaetoceros* sp. (which was isolated from the Mississippi River plume on cruise PE920412) to variation in light and dilution rate in semi-continuous cultures in the laboratory. Under strongly light limited growth conditions, such as those encountered by population in the river plume, cells were able to maintain high rates of growth and production through adjustment of cellular C and chl *a* content (Chen, 1994). C/N ratios decreased with light and with increased growth rates. The ratios which were encountered in the field (*e.g.*, approximately 7-8, by atoms) were similar to those which we found for the higher dilution rates and lowest light levels. This lends support to the idea that phytoplankton in the plume and shelf were growing at high relative growth rates and were adapted to low light levels (Chen, 1994).

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Figure Legends

Figure 1. Combined data for P_{\max}^B and α^B from all cruises plotted as a function of temperature (T). Closed symbols indicate results from measurements conducted during midday (1000-1400 h). Curved line is a subjective fit to the high values and is described by the equation, $P_{\max}^B = \exp(0.125 \cdot T)$. P_{\max}^B and α^B transformed to their natural logarithms were both significantly correlated with temperature ($r^2=0.157$, $P<0.001$, $N=363$ for $\ln(P_{\max}^B)$ and $r^2=0.153$, $P<0.001$, $N=363$ for $\ln(\alpha^B)$). Error bars indicate ± 1 standard error of the estimate and are shown only for the highest values.

Figure 2. Relationship of midday (1000-1400 h) values of P_{\max}^B and α^B to growth rate. Filled symbols indicate samples from the plume and open symbols were from shelf waters. Error bars designate ± 1 standard error.

Figure 3. Areal distributions of water column-integrated primary production estimated using a nonspectral photosynthesis-irradiance model (Lohrenz et al., 1992, and in prep.). A) July/August 1990, B) March 1991, C) September 1991, D) April/May 1992. Units are $\text{gC m}^{-2} \text{d}^{-1}$.

Figure 4. Relationship of water column-integrated primary production to salinity.

Figure 5. Comparison of observed water column-integrated primary production versus that estimated by satellite algorithm. Estimated production was computed as $(1/39) \cdot \text{PAR} \cdot \text{IC} \cdot \psi^*$, where ψ^* (g Chl^{-1}) is the chlorophyll specific cross-section under each trophic category and the appropriate value of water column-integrated chlorophyll (IC, g m^{-2}) (Prasad et al., in press). PAR is expressed in units of $\text{J m}^{-2} \text{d}^{-1}$ and the factor 1/39 accounts for the fact that the fixation of 1 mg of carbon corresponds to a storage of 39 J of PAR.

Table 1. Means and standard deviations (S.D.) of midday (1000-1400 h) values of photosynthetic parameters in the upper mixed layer. Units were as follows: P_{\max}^B (gC g Chl a^{-1} h $^{-1}$), α^B (g C [g Chl a h] $^{-1}$ [μ mol quanta m^{-2} s $^{-1}$] $^{-1}$), I_k (μ mol quanta m^{-2} s $^{-1}$). N=number of samples.

Cruise	P_{\max}^B		α^B		I_k		N
	Mean	S.D.	Mean	S.D.	Mean	S.D.	
September 1989	9.0	3.6	0.032	0.010	284	59	9
April 1990	10.4	3.4	0.041	0.014	281	127	7
July-August 1990	10.0	3.8	0.033	0.010	349	231	17
October 1990	11.3	5.3	0.049	0.024	246	74	10
March 1991	6.1	2.0	0.022	0.009	303	142	13
September 1991	23.0	5.5	0.055	0.015	429	83	7
April 1992	8.4	2.3	0.028	0.011	370	213	16
May 1992	5.4	2.8	0.018	0.004	325	221	5

Table 2. Photic zone integrated primary production (IPP; $\text{gC m}^{-2} \text{d}^{-1}$) for the simulated in situ primary production experiments conducted on each cruise in both the river plume and adjacent shelf study regions. Values are given for those experiments associated with the free-floating sediment trap array deployments. In addition, IPP results for the whole phytoplankton population and for the $< 8 \mu\text{m}$ size fraction determined with post-incubation size fractionation procedures are presented. n.d. = no data.

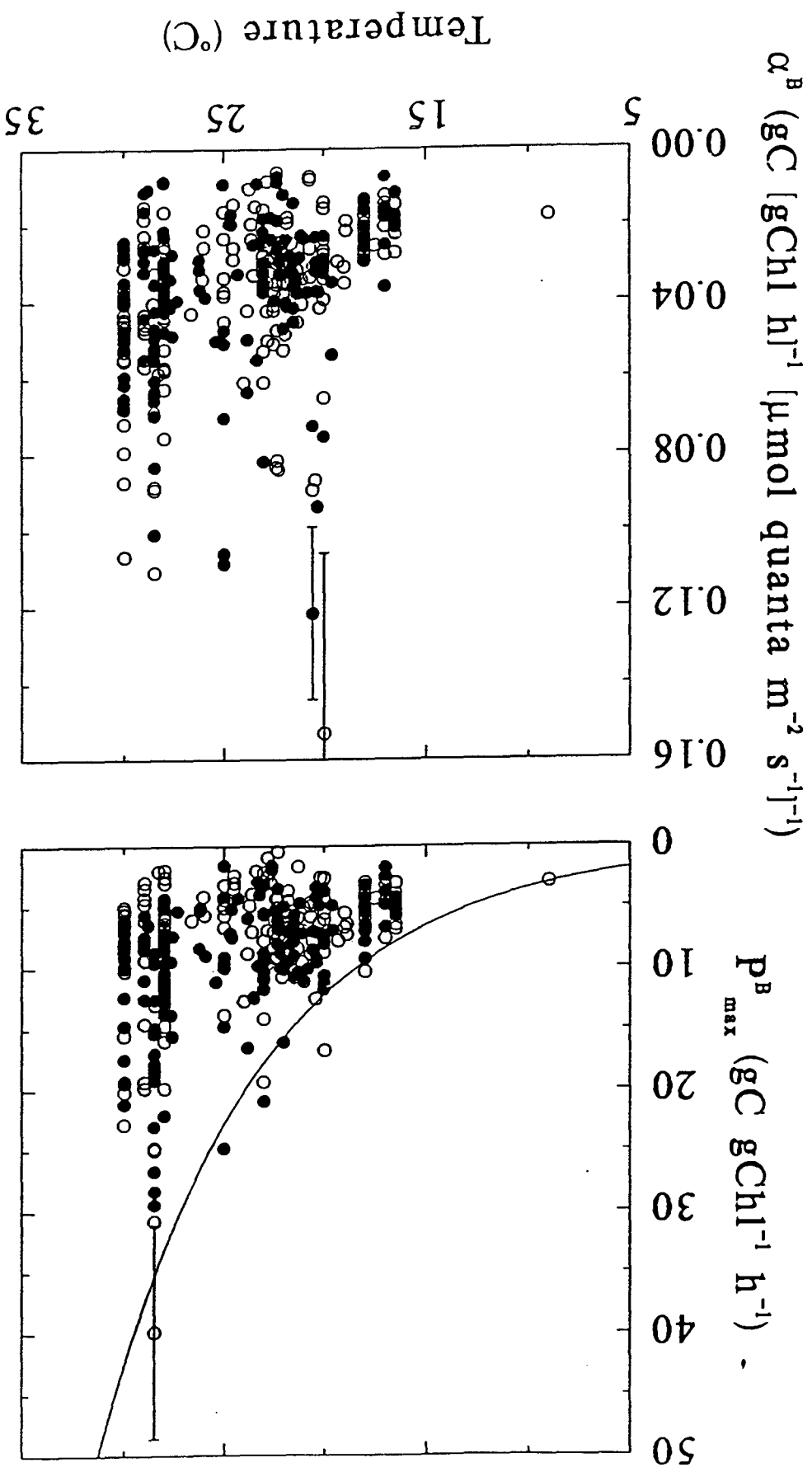
Cruise	Plume Region		Shelf Region	
	Total	$< 8 \mu\text{m}$	Total	$< 8 \mu\text{m}$
July/August 1990	8.17	5.32	1.89 - 3.02	1.13
March 1991	0.40 - 0.69	0.27	0.12 - 0.45	0.11
September 1991	0.86 - 1.65	0.67 - 0.99	0.17 - 0.36	0.16 - 0.39
May 1992	3.37 - 3.86	n.d.	0.31 - 1.07	n.d.

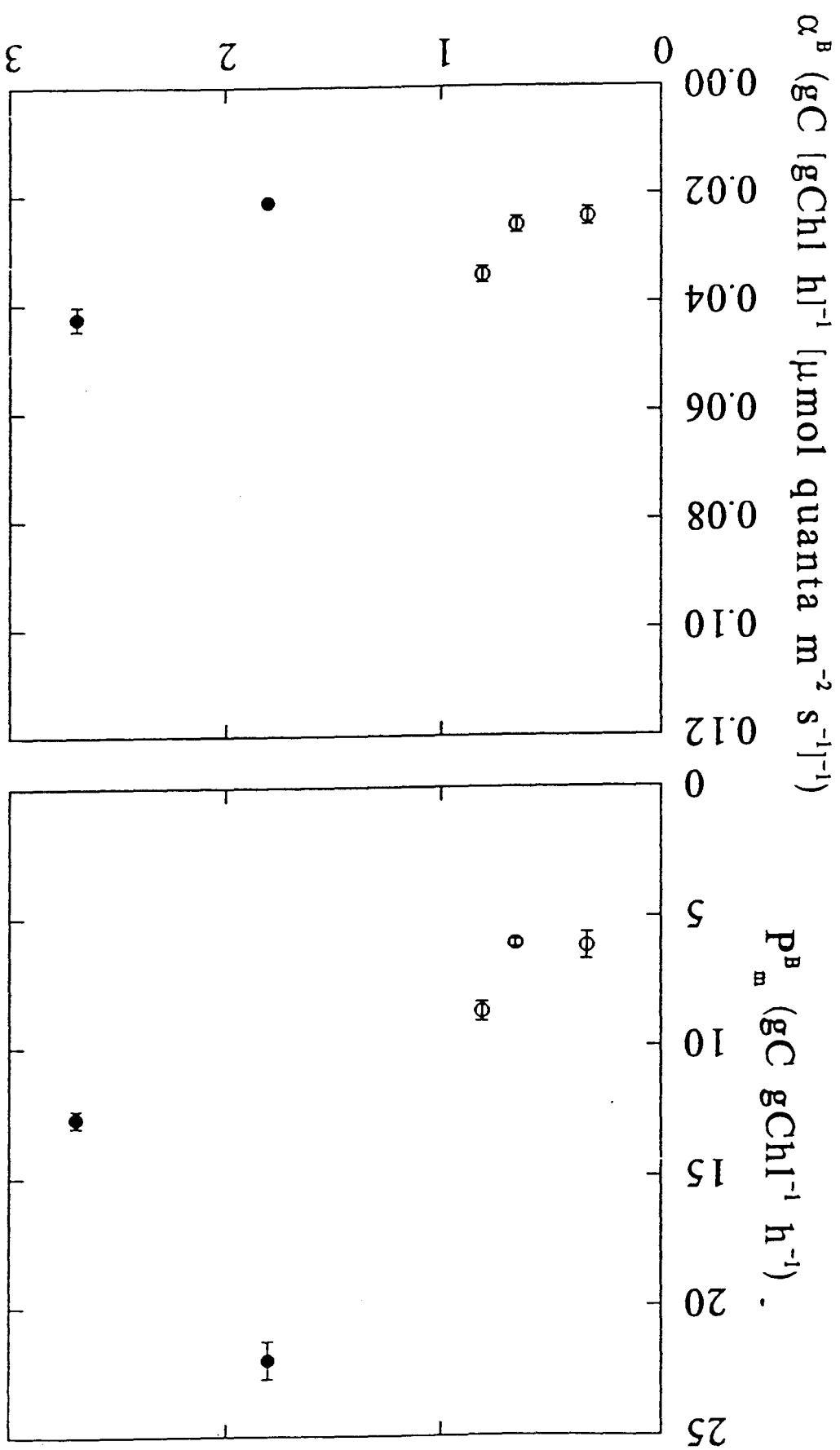
Table 3. Vertical flux of POC ($\text{gC m}^{-2} \text{d}^{-1}$) and PON ($\text{gN m}^{-2} \text{d}^{-1}$) out of the photic zone for the four NECOP cruises completed thus far. The standard error and number of replicate samples are given in parentheses.

<u>Cruise</u>	<u>Plume Region</u>	<u>Shelf Region</u>
July/August, 1990		
POC Flux	0.29 (0.02; n=3)	0.18 (0.01; n=4)
PON Flux	0.06 (0.003; n=6)	0.03 (0.002; n=8)
March, 1991		
POC Flux	0.95 (0.01; n=3)	0.32 (0.02; n=3)
PON Flux	0.16 (0.009; n=6)	0.05 (0.002; n=6)
September, 1991		
POC Flux	0.69 (0.02; n=12)	0.19 (0.01; n=6)
PON Flux	0.12 (0.003; n=12)	0.03 (0.001; n=6)
May, 1992		
POC Flux	1.80 (0.04; n=8)	0.40 (0.02; n=10)
PON Flux	0.27 (0.008; n=16)	0.07 (0.004; n=10)

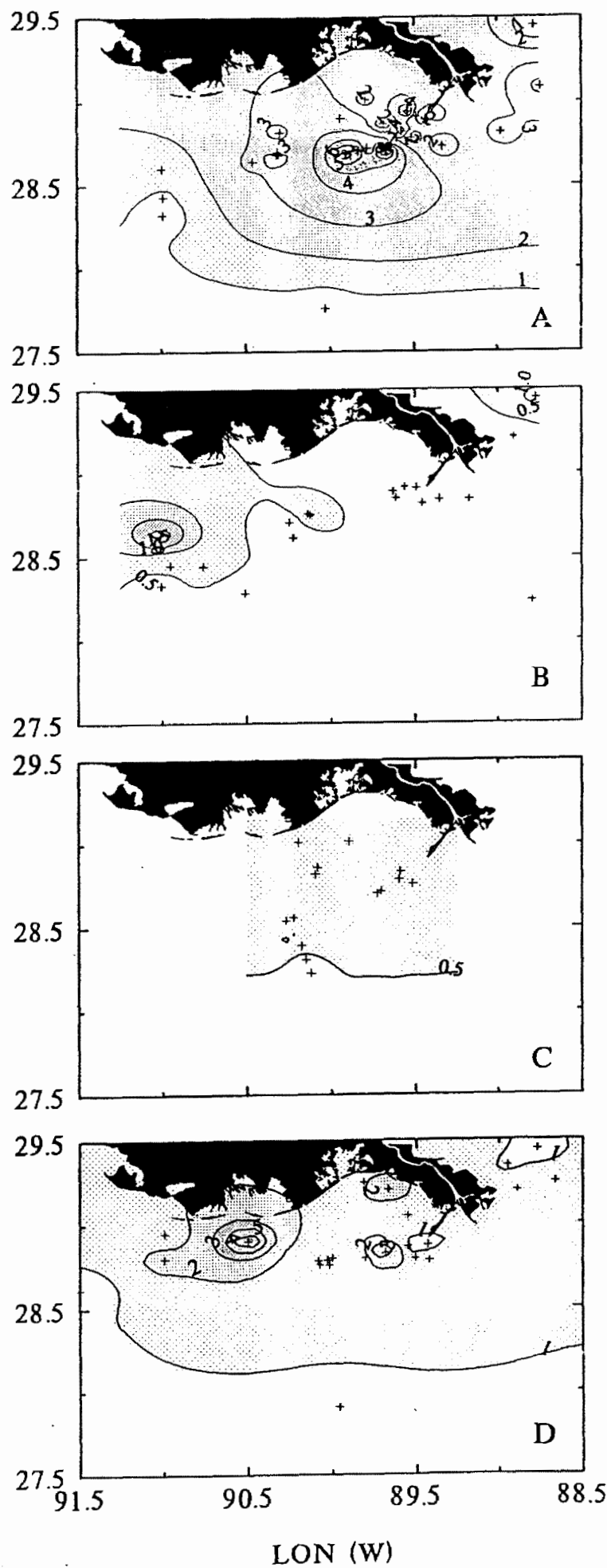
Table 4. The Pearson Correlation matrix for mean values of selected rate processes (integrated primary production, IPP; vertical export of POC, F_{POC} ; vertical export of PON, F_{PON} ; surface concentrations of NO_3^- , PO_4^{3-} , SiO_3^{2-} and chl *a*; mass of suspended particulate matter, SPM; diffuse attenuation coefficient over photosynthetically available radiation, K_{PAR} ; surface salinity, SAL; units are the same as in Table 3). Correlation coefficient values which exceed 0.707 (6 degrees of freedom) are considered to be significant at the 5 % level.

	IPP	F_{POC}	F_{PON}	NO_3	PO_4	SiO_3	Chl <i>a</i>	SPM	K_{PAR}	SAL
IPP	1.000									
F_{POC}	0.068	1.000								
F_{PON}	0.091	0.996*	1.000							
NO_3	0.934*	0.163	0.192	1.000						
PO_4	0.397	0.832*	0.802*	0.375	1.000					
SiO_3	0.968*	0.073	0.099	0.948*	0.349	1.000				
Chl <i>a</i>	0.865*	-0.008	-0.001	0.748*	0.433	0.753*	1.000			
SPM	0.387	0.883*	0.881*	0.440	0.900*	0.376	0.362	1.000		
K_{PAR}	0.576	0.471	0.484	0.661	0.576	0.468	0.591	0.506	1.000	
SAL	0.068	-0.029	-0.338	-0.233	0.114	-0.011	0.335	-0.065	-0.401	1.000





LAT (N)



Primary Production ($\text{gC m}^{-2} \text{d}^{-1}$)

